

Spatial patterns and environmental determinants of community composition of web-building spiders in understory across edges between rubber plantations and forests

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Abstract. Rubber plantations in Southeast Asia have expanded greatly in recent decades, thereby increasing the amount of edges bounding natural forests. In this study, we focused on the effects of rubber plantation-forest edges on species diversity and abundance of web-building spiders. We also aimed to reveal environmental determinants that influence such patterns. We visually searched and collected spiders within 85 quadrats from October to January (heavy rain period), and 160 quadrats from May to September (light rain period). The quadrats were placed in five sites representing rubber plantations, rubber plantation-forest edge, and forest interior up to 150 m from the edge. We examined understory characteristics, microclimate, and potential prey within each quadrat. Certain species were abundant in rubber plantations, others were abundant at the edge or within the forest, and others showed no pattern. Species richness was not related to the edge whereas species diversity and total abundance of the spiders was higher in the rubber plantation and decreased at the rubber plantation-forest edge and into the forest interior. Temperature range and average temperature appear to drive the distribution patterns of species diversity and total abundance. Characteristics of understory, namely dry twigs and seedlings also tended to affect such patterns. Temperature probably affected the spiders' ability to maintain favorable body temperatures whereas dry twigs and seedlings probably provide reliable web support and suitable refuges.

Keywords: Alpha diversity, Araneae, edge effect, peninsular Thailand, temperature

Recent deforestation in Southeast Asia has been rapid due to the large-scale expansion of rubber plantations (Li et al. 2007). Replacing natural forests by rubber plantations can reduce biodiversity through habitat fragmentation as well as forest degradation (Zhai et al. 2012). An increase of edge habitats and effects of edges are among the phenomena caused by the fragmentation; they may affect the distributions and the interactions of organisms in the ecosystem (Ries et al. 2004). Despite the situation mentioned above resulting in an increase of rubber plantations-forest edges, studies on the effect of this edge type on biodiversity are sparse.

Spiders are reliable bioindicators of environmental change in tropical ecosystems (Malumbres-Olarte et al. 2013). Web builders are sit-and-wait spiders that directly use webs for capturing prey; they stay within the small range of their webs, so have small home ranges (Miyashita et al. 1998). They are highly sensitive to environmental changes (Lessard et al. 2010). Accordingly, the web builders appear to be suitable animal models to assess edge effects, especially in small-scale ecosystems.

A number of studies have shown edge effects on arthropod abundance and richness (Bogyó et al. 2015; Lacasella & Zapparoli 2015). Their patterns along edge gradients varied depending on taxa or vegetation type (Albrecht et al. 2010; Rykken et al. 2011). Some studies reported no detectable edge effects on the abundance of several groups of arthropods (Jabin et al. 2004). On spider diversity, most studies have shown positive edge effects (Gallé & Fehér 2006; Rodrigues et al. 2014) while a few studies have shown negative edge effects (Rodrigues et al. 2014) or no edge effects (Pearce et al. 2005). Also, a few studies have shown intermediate effects on spider diversity whereby at a plantation/pasture edge, spiders were

more abundant relative to the forest plantation, but less abundant relative to the grass pasture (Downie et al. 1996). Specific studies on distribution patterns of web-building spider assemblages along edge gradients and environmental variables influencing these patterns are described by Baldissera et al. (2004, 2008). The edge between *Araucaria* forest and *Pinus* plantation did not significantly affect richness and abundance of web-building spiders (Baldissera et al. 2008), while the richness and abundance were positively affected by the edge between pasture and *Araucaria* forest. The latter pattern was positively influenced by vegetation species richness (Baldissera et al. 2004).

In this study we focused on the effects of rubber plantation-forest edge on web-building spiders. Our first objective was to investigate changes in species diversity, richness, and abundance of the spiders from rubber plantations across edges toward forest interiors. The edge effects can occur both at community and species levels of spiders. At a community level, we expected that the spider diversity, richness, and total abundance would be highest in rubber plantations, where the understory habitat has relatively high complexity and density, and that it would decrease at the edge toward the forest which had a relatively sparse understory in our study area. At the species level, we expected that abundance of different species would vary in response to edge because of differences in microhabitat preference. Although it is broadly known that environmental conditions influence spiders (Entling et al. 2007), the key environmental variables are not well understood, especially in the inter-habitat transition zones. Consequently, our second objective was to analyze environmental variables determining the patterns of spiders along the edge gradients. Based on previous research mentioned above, we

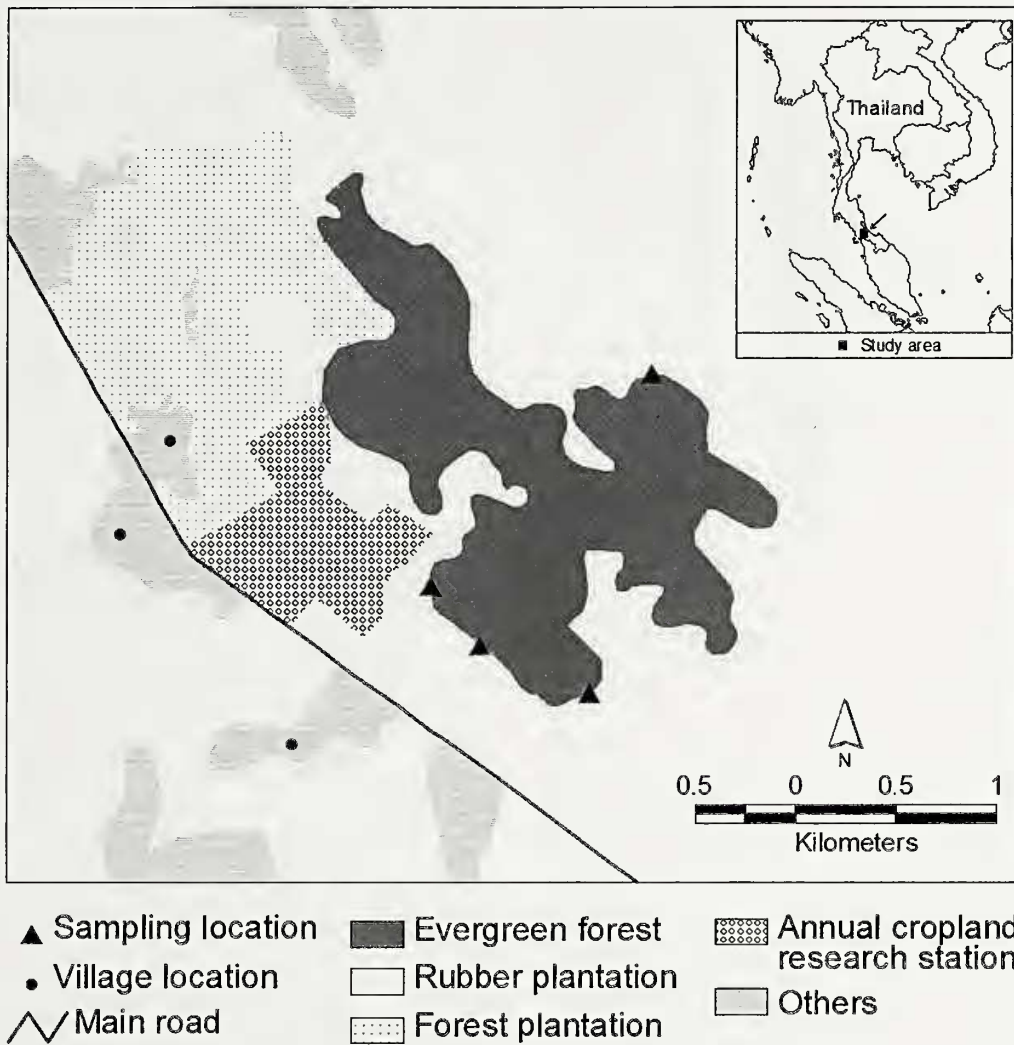


Figure 1.—A map of the study area, including the Khuan Khao Wang Forest Park (the dark grey component), and the rubber plantation zone (the white component). The black triangular symbols indicate the sampling locations where belt transects were set to extend from the rubber plantation into the forest.

predicted that vegetation complexity and density of understory would be the primary determinants.

METHODS

Study area.—The study was carried out in Khuan Khao Wang Forest Park (area = 3.26 km²), Hat Yai District, Songkhla Province, southern Thailand (6°59'N, 100°18'E, 200 m a. s. l.) (Fig. 1). This forest park is a secondary forest remnant composed of semi-evergreen lowland trees, and has been naturally reforested for about 25 years since the termination of the logging concession. Logging began in 1970 and was terminated a few years later. Then, in 1995, the forest was assigned protected area status. The dominant trees in the forest park were *Barringtonia* spp., *Diospyros* spp., *Dipterocarpus alatus* Roxb. Ex G. Don, *Eugenia* spp., *Fagraea fragrans* Roxb., *Intsia* spp., *Lithocarpus* spp., *Morinda* spp., *Pterocarpus* spp., and *Shorea* spp. This protected area has a hill (200 m a. s. l.) and a few seasonal streams, and is surrounded by rubber plantations, forest plantations, a small area of cropland, a few palm plantations, and houses. Outside

the boundaries of the forest park, the monoculture rubber plantations are dominant. The forest plantations have *Dipterocarpus alatus* Roxb. ex G. Don, *Intsia paleubanica* Miq., *Hopea odorata* Roxb., *Shorea roxburghii* G. Don, *Azadirachta excels* (Jack) Jacobs, and *Casuarina equisetifolia* J.R. & G. Forst. Most of the rubber plantations are mature (7–25 years old) with a canopy height of approximately 14 m; the rubber trees within each plantation are about the same age and height. Generally, the rubber trees are planted at 3 m intervals within each row, and 7 m spacing between the rows. The understory vegetation consists of grasses, sedges, herbs, ferns, vines, woody seedlings, and lianas, which are significantly denser in the rubber plantations than in the forests. Generally, the woody seedlings are dominant in the forest understory, while grasses are almost absent. In contrast, various species of grasses and herbs are the dominant vegetation in the rubber plantations. Human disturbances, including mowing and latex tapping, take place regularly in the rubber plantations. Traditionally, farmers slash or mow the understory in their plantations once a year, and they routinely walk the tracks along the rubber tree rows in order

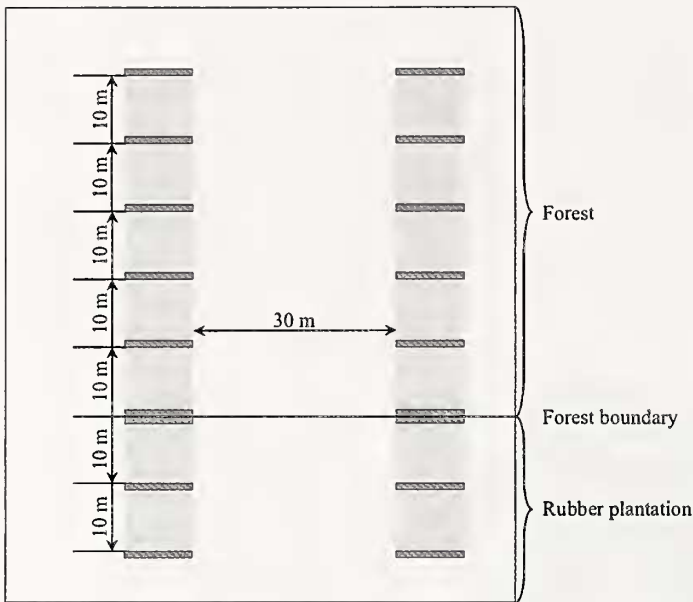


Figure 2.—The arrangement of 15×2 m sampling plots, crossing the forest boundary and extending to the forest interior and the rubber plantation. The understory, sapling, and tree densities were assessed by sampling these plots.

to tap the latex. The mean annual precipitation during 2003–2012 was 1890.3 ± 122.4 mm (mean \pm SE). Generally, there are two seasons in the study area: dry and wet. Based on Mohr (1944), the dry season is from February to mid-April (mean monthly precipitation across 2003–2012 = 58.3 ± 15.2 mm). The wet season can be divided into two periods: the period of light rain from May to September (mean monthly precipitation across 2003–2012 = 86.1 ± 7.7 mm), and the period of heavy rain from October to January (mean monthly precipitation across 2003–2012 = 309.9 ± 34.6 mm) (Rattaphum meteorological station, unpublished data).

Edge determination.—The vegetation characteristics were assessed along paths from the rubber plantation into the forest, in order to determine the position and width of the edge zone between the rubber plantation and the forest. We selected rubber plantations of at least 15 years of age that had not had herbicides or insecticides applied for the last 10 years (based on interviews of rubber farmers), and had not had understory mowing during the last 6 months. We identified the line across which the vegetative contrast was strongest, approaching the forest from the rubber plantation (Cadenasso et al. 2003). We established belt transects of 15 m width, extending 20 m into the rubber plantation and 50 m into the forest from the forest boundary (the contrast line), spaced 30 m apart. We outlined 15×2 m plots in the rubber plantation and in the forest, on both sides of the forest boundary and then at every 10 m (Fig. 2), and counted saplings and trees (woody plants > 1.5 m tall) in the plots. We further outlined 1×1 m subplots at the center, as well as in the upper right and lower left corners of each plot, and assessed the understory in these subplots (see “Assessment of environmental variables” for details).

Study design.—We applied an interrupted belt transect sampling method on the rubber plantation across the edge toward the forest interior. Each transect was at least 50 m away from the outer bounds of the rubber plantation and the

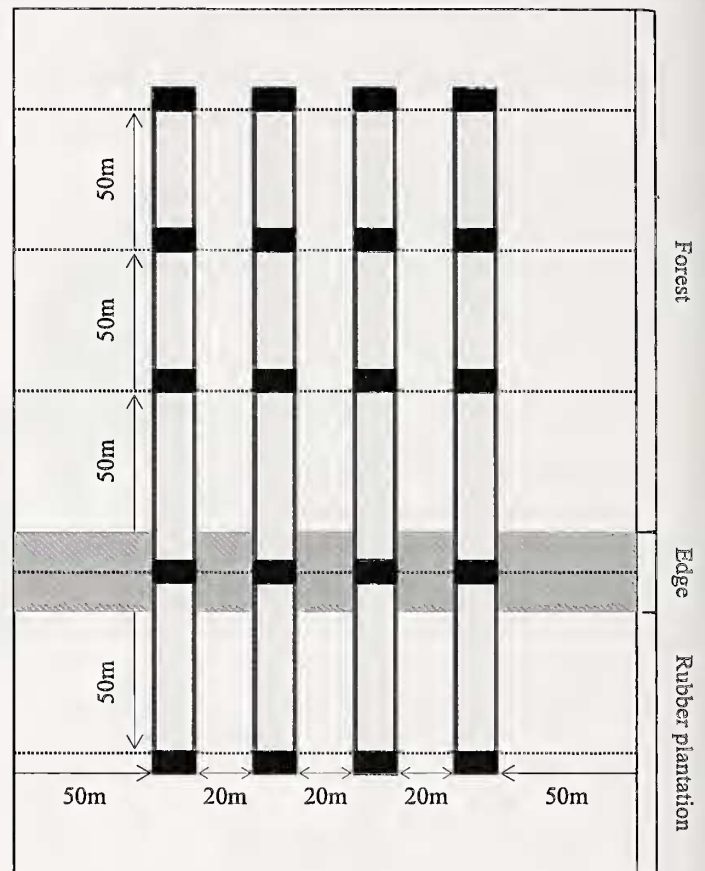


Figure 3.—The arrangement of 3×2 m quadrats for collecting spiders and assessing environmental variables at each site along belt transects spaced 20 m apart during the first session of data collection. A site was located at the edge, and others at 50 m from the edge into the rubber plantation, and 50, 100, and 150 m from the edge into the forest. During the second session of data collection, the same five sites along the transects were used, but this time 1×1 m quadrats were spaced 10 m apart along the transects.

forest (horizontal distance shown in Fig. 3). We conducted the study in two sessions. The first session, from October 2008 to January 2009 (in the period of heavy rain) was to examine whether the edges affect the distribution of spiders. We laid 17 belt transects (3 m wide) spaced 20 m apart, and placed 3×2 m quadrats to collect spiders at five sites along each transect. The sampling sites on the transects were: at the edge, 50 m from the edge into the rubber plantation (RP); and 50 m (F050), 100 m (F100), and 150 m (F150) from the edge into the forest (Fig. 3). The second session, from June to September 2012 (during the light rain period) was to confirm an existence of edge effects and assess environmental determinants of spider distribution along the edge gradients. Because the heavy rains obstructed spider collection, we conducted data collecting of the second session in the light rains instead of the heavy rains. Spiders and data on environmental variables likely to affect their distribution patterns (see “Spider sampling and identification” and “Assessment of environmental variables” for details) were collected. We laid 32 belt transects (1 m wide) spaced 10 m apart, and placed 1×1 m quadrats at every 50 m for five sites along each transect, in a similar arrangement as for the first session but at a different place to avoid

pseudoreplication (Fig. 3). We downsized the sampling quadrats in the second session, to be able to complete both spider and environmental variable samplings of each transect within the same day. In the rubber plantation, we placed sampling quadrats only between the rows of rubber trees and away from tracks, in order to avoid disturbance by walking farmers.

Spider sampling and identification.—Within each quadrat, we found spiders during the daytime, on days without rain, from the ground up to 1.5 m height visually surveying all understories, saplings, trees, stones, and dry leaves/twigs/branches. We searched for spiders for 25 min. in the 3×2 m quadrats, and for 10 min. in the 1×1 m quadrats, to collect as many as possible. The time taken to collect spiders was excluded from the sampling time. Along each transect we randomized the order of quadrats for collecting spiders, on every collection day, to avoid temporal confounding effects related to the time of a day. Kleptoparasitic spiders were not included in this sampling. We identified mature spiders mainly on the basis of morphological characteristics, to the extent possible. For certain spiders, we used DNA analyses for identification, focusing on the mitochondrial cytochrome oxidase subunit I sampled from specimens preserved in 75% ethanol. All the procedures for DNA extraction, polymerase chain reaction, and sequencing, followed Tanikawa (2012), except for the DNA extraction kit. We used a FavorPrep Tissue Genomic DNA Extraction Mini Kit (Favorgen Biotech Corp, Ping-Tung, Taiwan). We applied the nomenclature after Platnick (2014). Specimens were stored in 75% ethanol in vials, and deposited in the Princess Maha Chakri Sirindhorn Natural History Museum at Prince of Songkla University, Hat Yai, Thailand.

Assessment of environmental variables.—We collected data on vegetation structure for edge determination. Although vegetation structure is well known to influence web-building spiders, microclimate (Sattler et al. 2010) and potential prey (Halaj et al. 2000) have been also suggested. Accordingly, to analyze environmental determinants of distribution patterns of the spiders along the edge gradients, we measured vegetation structure, microclimate and potential prey availability for evaluating determinants of spider distribution patterns (in the second session).

Vegetation structure: For edge determination, we counted the number of stems or trunks of trees and saplings in each plot. We quantified the density of understory vegetation by counting leaves of grasses/sedges/ferns, all stems of vines and lianas, and primary stems of herbs/seedlings in each subplot.

For determinants of spider distribution patterns, we assessed densities of grasses, sedges, herbs, ferns, vines, lianas, seedlings, saplings, and trees by counting their buttresses, trunks, branches, stems, twigs, rachises, leaves, or inflorescences within each quadrat. We then obtained a measure of vegetation complexity from the combination of all plant categories above (McCoy & Bell 1991). We measured the cover percentage of canopy by sighting with a cardboard tube with a crosshair through the canopy. This was repeated at the center and in every corner of each quadrat (simple point intercept method: James & Shugart 1970). We estimated the cover percentage of litter on the ground, and measured the litter depth in all four corners and at the center of each

quadrat. We counted the numbers of stones on the ground and also counted arboreal dead leaves/twigs/branches in the quadrats up to a height of 1.5 m.

Microclimate: We programmed data loggers, HOBO® U12 Temp/RH/Light/External Data Logger - U12 - 012 (Onset Corporation, Bourne, MA), to record temperature, relative humidity, and light intensity at 30 min intervals, and placed them in transparent plastic rain shelters at 1 m height in every site along each transect, for a continuous period of 48 h. In each site, we randomly selected two from five points, four corners and at the center, within each quadrat. We also randomized the order of such two points for measuring microclimate in a quadrat and placed a data logger for 24 h at point one and moved to point two for continuing measurement another 24 h. From the resulting data, we calculated the daily ranges (maximum – minimum) and average values for each of the microclimate variables (Vandergast & Gillespie 2004).

Prey availability: For insect sampling, we applied sticky traps made from 15×15 cm transparent plastic pads coated with sticky glue. Within each quadrat along the transects, we placed the traps above the ground at 0, 0.5, 1.0, and 1.5 m heights, for 72 h. Insects captured by these traps were identified to order level following Borror et al. (1989). The trapped insects were counted, and their body lengths were measured. Dry biomass of each insect was estimated using the formula $W = 0.0305L^{2.62}$, where W is the dry mass in mg, and L is the length in mm (Lumsden & Bennett 2005).

Statistical analysis.—We applied the Shannon-Wiener diversity index to provide a measure of relative diversity of the spiders (Magurran & McGill 2011). To standardize species richness of spiders across sampling plots, we estimated rarefied species richness by using a function from the library “vegan” in R (Oksanen 2015). To designate dominant species, we calculated the proportion of individuals of each species divided by total number of individuals. We defined dominant species as those making up $\geq 3\%$ of individuals in the sample following Spiller & Schoener (1998). To compare the differences in spider diversity, species richness, and abundance of species in total and each dominant species between sites, we used one-way ANOVA, where “site” was used as a fixed factor. We checked the normality of spider data, using the Wilk-Shapiro test, and tested homogeneity of variance using Bartlett’s test. The dependent variables were transformed by natural logarithms in cases where the data lacked normality or homogeneity of variance. We used Kruskal–Wallis tests when normality was not met. For post hoc multiple comparison tests, we applied Tukey’s test following one-way ANOVA and Mann-Whitney U-test following Kruskal–Wallis tests. Because we used the Mann-Whitney U-test, which is a pairwise comparison for simultaneous inference, we adjusted the significance level by using the Dunn-Sidak procedure, in order to reduce the possibility of Type I errors (Quinn & Keough 2002). For dominant species, since their occurrences are not independent and we repeatedly applied the test on different species, we used Bonferroni correction to reduce the possibility of Type II errors (Cabin & Mitchell 2000). For spider diversity and total abundance that demonstrate patterns along edge gradients, we evaluated key environmental variables influencing the patterns. For abundance of the dominant species that

also demonstrated patterns along the edge gradients, we could not evaluate key environmental variables influencing their patterns because of too many zeros in the response variable data set.

We applied a Gaussian generalized linear model (GLM) with an identity link to evaluate the relationship between the environmental variables and spider diversity. For the spider abundance of all species combined, we applied zero-inflated models (Zuur et al. 2009), i.e., the ZIP or the ZINB models using the "psel" library in R (Jackman 2012). This approach was appropriate because our data had an excessive number of zeros. We used the MuMIn package in R (Barton 2012) to construct a set of alternative full models. We applied the Akaike Information Criterion (AIC) for model selection and presented only the best models (Burnham & Anderson 2002). To evaluate whether there are effects of spatial autocorrelation in parameters, we assessed spatial autocorrelation of the final model with correlograms using a spline function in the ncf package in R (Bjørnstad 2015). There was no significant spatial autocorrelation. We used each best model to predict the values of spider diversity and total abundance, as functions of the environmental variables, to assess the effect sizes of these variables (Martin et al. 2005). We computed the percentage of the effect size of each key environmental variable on spider diversity and the total abundance following Pilosof et al. (2012), dividing the predicted minimum value by the predicted maximum value of spider diversity and total abundance, and multiplying the result by 100. We performed all the analyses in R v.3.1.0 (R Core Team 2013).

RESULTS

Vegetation change and edge determination.—Understory density was higher in the rubber plantations than in the forests, decreasing sharply within 10 m of the forest boundary (from RP10 to F00, Fig. 4A). The tree density was lower in the rubber plantation than in the forest, and had a steep increase at the transition zone to the forest (from RP00 to F00) (Fig. 4B). Plant density changed conspicuously from 12 m within the rubber plantation to 2 m within the forest, measured from their boundary, and this defined an edge zone of approximately 14 m width (Figs. 2, 4).

Distribution of environmental variables.—The temperature range and seedling density differed significantly between the sites (Kruskal–Wallis tests, temperature range: $H_4 = 54.3$, $P < 0.001$; seedling density: $H_4 = 24.3$, $P < 0.001$, Fig. 5). The temperature range was wider at the RP than at the edge and in the forest. Likewise, seedling density in the RP was significantly greater than at the edge and in the forest. The average temperature and dry twig density did not differ significantly between the sites (Kruskal–Wallis tests, average temperature: $H_4 = 9.6$, $P = 0.05$; dry twig density: $H_4 = 8.7$, $P = 0.07$, Fig. 5).

Distribution pattern of web-building spiders.—During the first session (heavy rains), a total of 1753 spiders were collected including 917 (52.3%) juveniles and 836 (47.7%) adults. Adults belonged to 67 species of 14 families. Nine species were considered dominant, and these nine species accounted for 74% of total abundance. During the second session (light rains), a total of 908 spiders were collected, including 611 (67.3%) juveniles and 297 (32.7%) adults. Adults belonged to

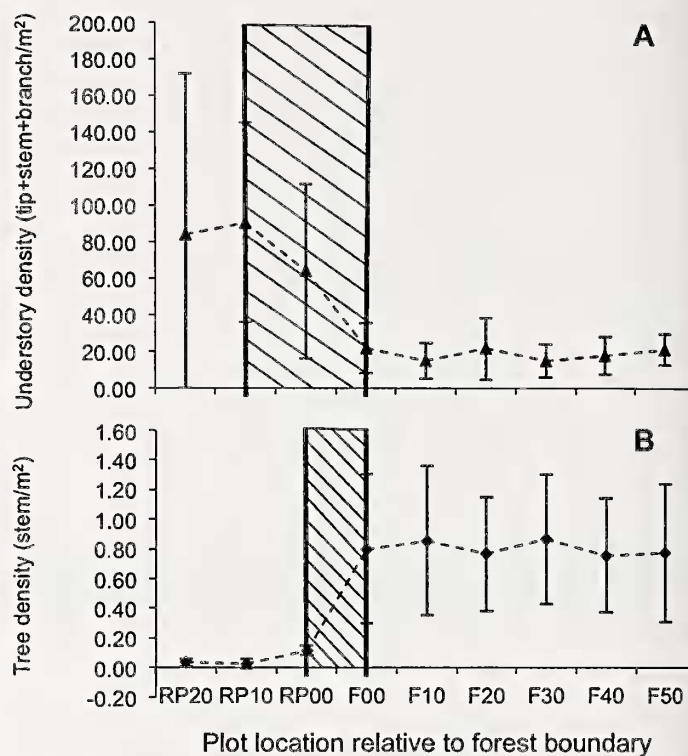


Figure 4.—Plots of the distribution of understory (A) and the tree density (B) along the transect extending from rubber plantation (RP) into forest (F). RP00, RP10, and RP20 are at distances 0, 10, and 20 m from the forest boundary to the rubber plantation, while F00 to F50 are at distances 0 to 50 m into the forest from the boundary. Points are means. Whiskers show SE.

50 species of 12 families. Nine species were considered dominant, accounting for 71% of total abundance.

During the first session (heavy rains), significant differences between rubber plantation and forest sites were found in *Crassignatha* sp2, Araneidae gen. sp3, and Mysmenidae gen. sp3 (Table 1). The abundance of *Crassignatha* sp2 was significantly higher in the F150 than in RP (Fig. 6A). The abundance of Araneidae gen. sp3 was significantly higher at the edge than at RP and at F150 (Fig. 6B). The abundance of Mysmenidae gen. sp3 was significantly higher at RP than at the edge, F050, and F150 (Fig. 6C). The abundance of other dominant species, namely, Araneidae cf. *Nemoscolus* sp., *Leucauge argentina* (Hasselt, 1882), Linyphiidae gen. sp1, Mysmenidae gen. sp1, *Octonoba* sp1, *Zona dibaiyin* Miller, Griswold & Yin, 2009, did not differ significantly between rubber plantation and forest sites.

During the second session (light rains), we found significant differences between the sites in Araneidae cf. *Nemoscolus* sp., Mysmenidae gen. sp1, and Theridiidae gen. sp1 (Table 1). The abundance of Araneidae cf. *Nemoscolus* sp. was significantly higher in the F150 than in RP (Fig. 6D). The abundance of Mysmenidae gen. sp1 was significantly higher at the edge than at F100 (Fig. 6E). The abundance of Theridiidae gen. sp1 was significantly higher at the rubber plantation than in the forest (Fig. 6F). The abundance of other dominant species, namely, Araneidae gen. sp3, *Belisana khaosok* Huber, 2005, Lycosidae gen. sp., Linyphiidae gen. sp1, Symphytognathidae gen. sp1,

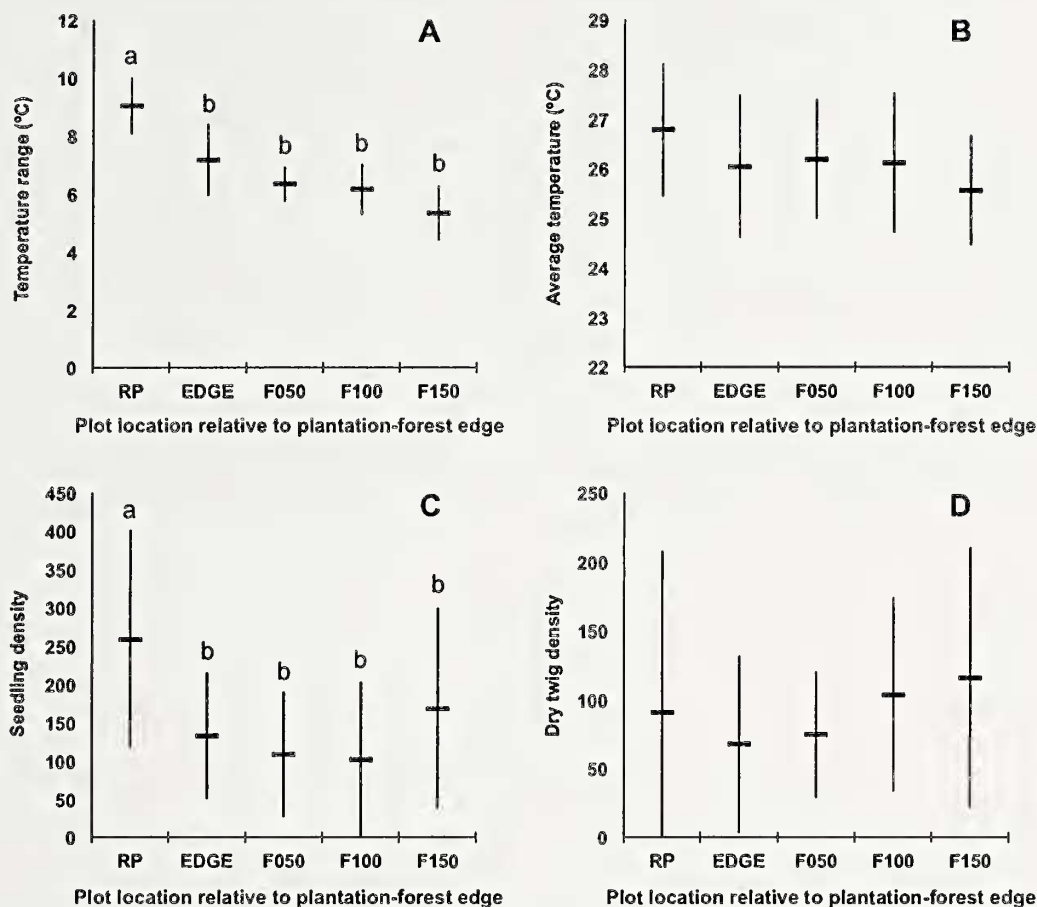


Figure 5.—The comparison of key environmental factors, temperature range (A), average temperature (B), seedling density (C), dry twig density (D), across the edge from rubber plantation into the forest. Bars are means. Whiskers are SE. Different letters indicate significant differences.

Table 1.—A list of dominant spider species, total abundance, and results of Kruskal–Wallis test ($df=4$) comparing the abundance of each species between sites from rubber plantation and forest. Bold letters indicate significant differences between sites following a *post hoc* test.

Species	Total abundance	Kruskal–Wallis test	
		H	P
Heavy rain period			
Araneidae cf. <i>Nemoscolus</i> sp.	67	5.4	0.25
Araneidae gen. sp3	33	19.9	< 0.001
<i>Crassignatha</i> sp2	93	21.9	< 0.001
<i>Leucauge argentinia</i> (Hasselt, 1882)	38	11.9	< 0.05
Linyphiidae gen. sp1	74	2.4	0.66
Mysmenidae gen. sp1	229	3.6	0.46
Mysmenidae gen. sp3	21	31.2	< 0.001
<i>Octonoba</i> sp1	23	6.2	0.19
<i>Zoma dibaiyin</i> Miller, Griswold & Yin, 2009	39	14.7	< 0.01
Light rain period			
Araneidae cf. <i>Nemoscolus</i> sp.	32	16.6	< 0.001
Araneidae gen. sp3	9	0.8	0.94
<i>Belisana khaosok</i> Huber, 2005	10	6.1	0.19
Lycosidae gen. sp.	12	8.3	0.08
Linyphiidae gen. sp1	16	4.7	0.31
Mysmenidae gen. sp1	54	15.3	< 0.005
Theridiidae gen. sp1	35	27.3	< 0.001
Symphytognathidae gen. sp1	10	9.5	0.05
Symphytognathidae gen. sp2	34	9.5	0.05

Symphytognathidae gen. sp2, did not differ significantly between the sites (Table 1).

During the first session (heavy rains), the diversity of spiders differed significantly between the sites (Kruskal–Wallis test, $H_4 = 14.9$, $P < 0.01$). It was significantly higher in the RP than at F050 (Fig. 7A). Species richness and total abundance of spiders did not differ significantly between the sites (one-way ANOVA, richness: $F_{4, 95} = 1.0$, $P = 0.41$; abundance: $F_{4, 95} = 1.1$, $P = 0.36$, Fig. 7B, C). During the second session (light rains), the diversity and total abundance of spiders differed significantly between the sites (diversity: one-way ANOVA, $F_{4, 95} = 3.9$, $P < 0.01$; abundance: Kruskal–Wallis test, $H_4 = 16.4$, $P < 0.01$). The diversity of spiders was significantly higher at RP than at F100 (Fig. 7D). The abundance was significantly higher both at RP and at EDGE than at F100 (Fig. 7F). Species richness of spiders did not differ significantly between the sites (Kruskal–Wallis test, $H_4 = 4.0$, $P = 0.40$, Fig. 7E).

Variables influencing the distribution pattern of web-building spiders.—The average temperature and the temperature range were significant variables affecting total abundance and diversity of spiders (Table 2). Not only temperatures but also seedlings and dry twigs affected the total abundance and the diversity. The models suggest that a wider temperature range contributed to the increase in total abundance and diversity of spiders, while increasing the average temperature reduced the

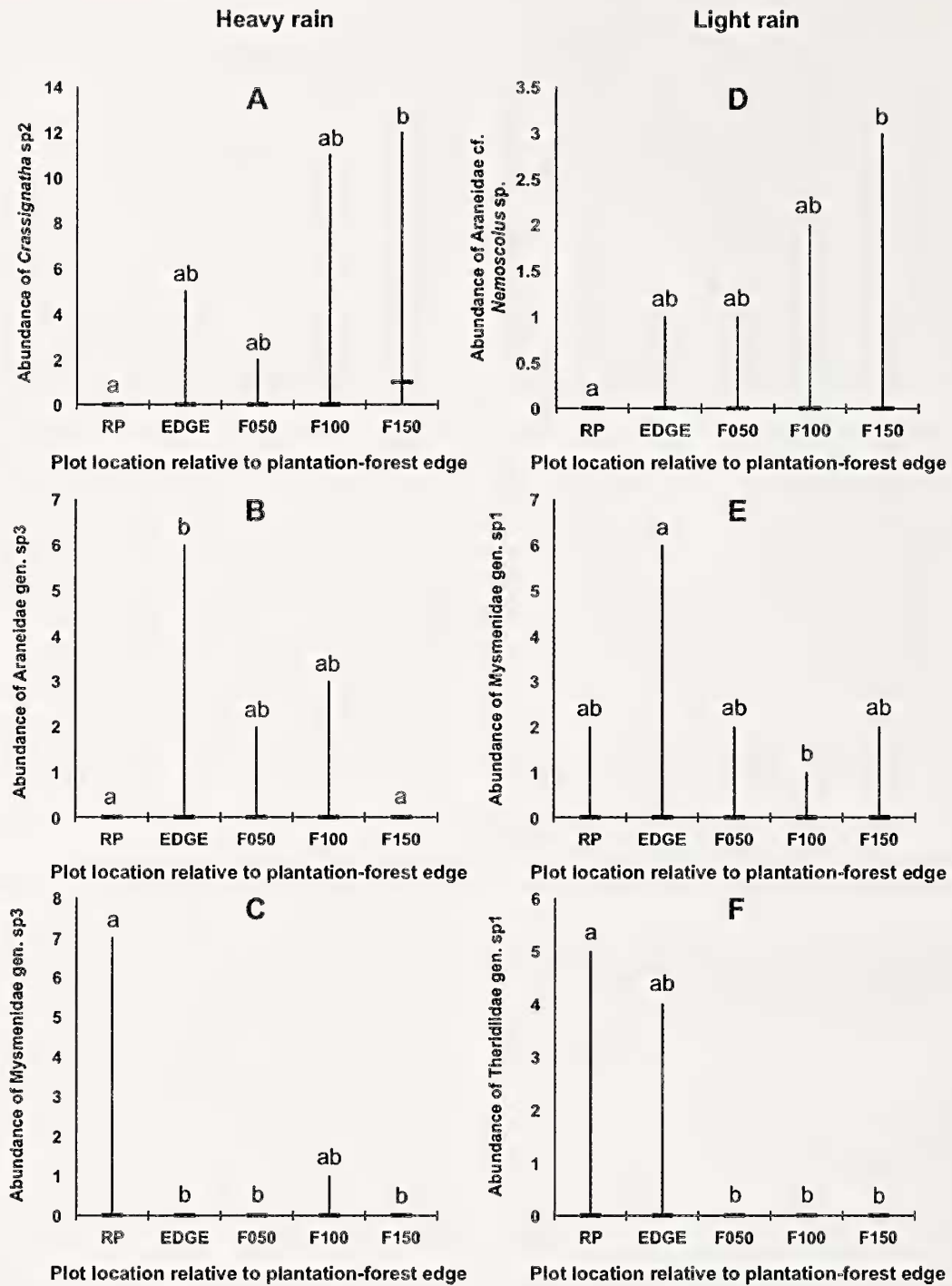


Figure 6.—Median values with range of abundance for the dominant species of spiders from rubber plantation into forest. Dashes are medians. Whiskers show ranges. Different letters indicate significant differences.

total abundance and the diversity. The numbers of seedlings and dry twigs positively influenced the total abundance and the diversity (Table 2). The zero-inflated negative-binomial model that we applied for total abundance of spiders did not show significant results (dry twig: $\beta = -0.274$, $Z = -0.963$, $P = 0.336$). The fitted GLM explained 19.3% of deviance in the diversity (Table 2). Species diversity was increased by 69% (from 1.15 to 1.67), 46% (from 1.24 to 2.71), and 47% (from

1.22 to 2.60) by temperature range, seedling abundance, and number of dry twigs, respectively. The diversity declined by 62% (from 1.68 to 1.05) with average temperature (Fig. 8). Temperature range, seedling abundance, and dry twigs increased the total abundance 22% (from 0.85 to 3.91), 9% (from 1.28 to 14.10), and 8% (from 1.15 to 14.15), respectively. The total abundance declined by 20% (from 3.47 to 0.68) with average temperature (Fig. 9).

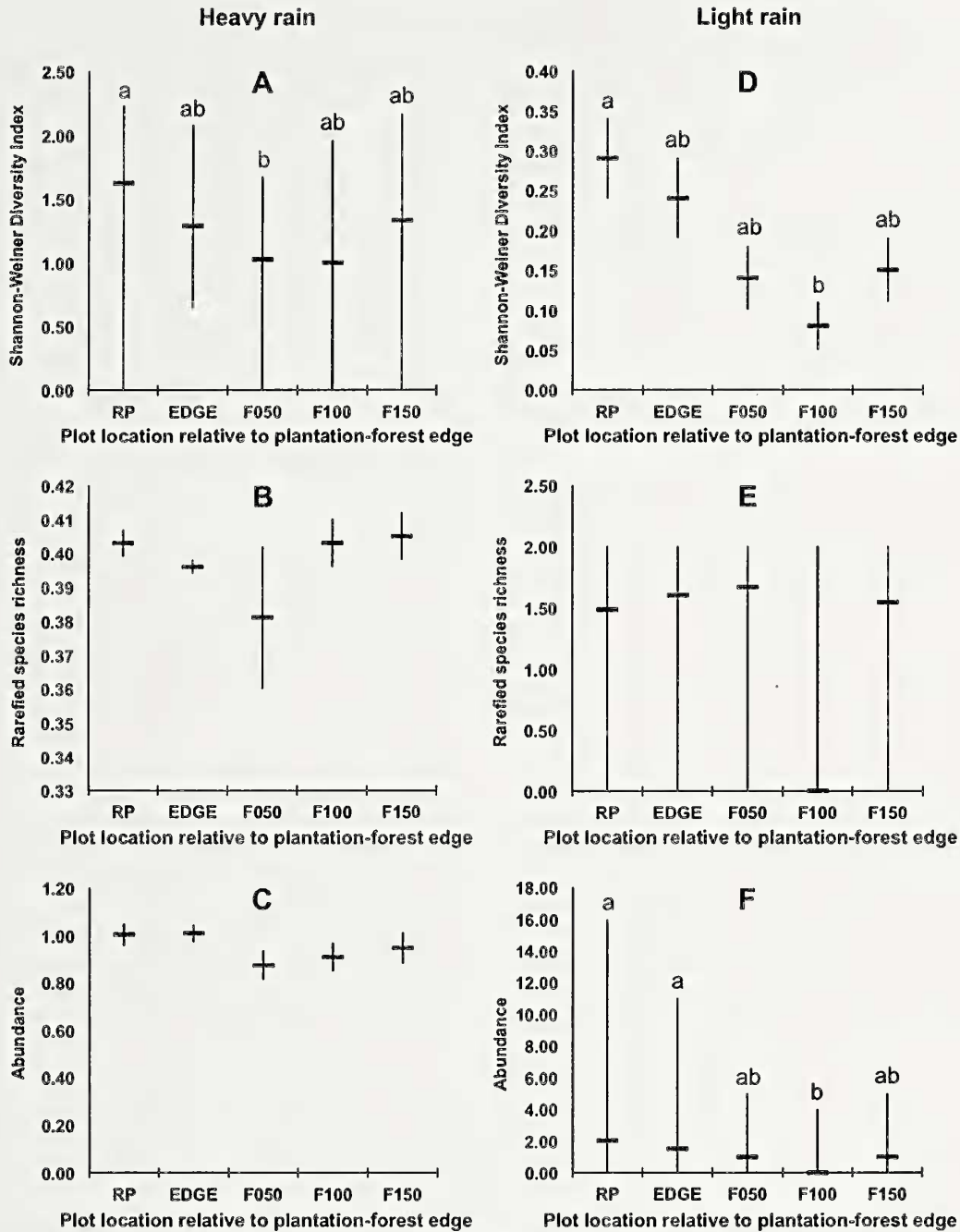


Figure 7.—The species diversity, the species richness, and the total abundance of web-building spiders from rubber plantation into forest. Mean values with SE are shown for the species diversity (D) during light rain period, and for the species richness (B) and the total abundance (C) during heavy rain period; dashes are means; whiskers are SE. Median values with range are shown for the species diversity (A) during the heavy rain period, and for the species richness (E) and the total abundance (F) during the light rain period; dashes are medians; whiskers indicate the range. Different letters indicate significant differences.

DISCUSSION

Effect of edge on the distribution pattern of web-building spiders.—Certain species of web-building spiders indicated the existence of the edge effect. As in previous studies (Baldissera et al. 2004; Vandergast & Gillespie 2004), the pattern of edge responses in abundance of spiders varied among different species. Edge influenced spider distribution in periods of both heavy and light rain, despite the fact that different taxa occurred in each period.

Crassignatha sp2, Mysmenidae gen. sp3, and Theridiidae gen. sp1, which were found only in a single period and responded to the edge, are probably sensitive to environmental change. The effects of edge on Araneidae gen. sp3, Araneidae cf. *Nemoscolus* sp., and Mysmenidae gen. sp1, which were found in both sampling periods varied. Araneidae gen. sp3 was influenced by edge in the period of heavy rain but not in the period of light rain. Araneidae cf. *Nemoscolus* sp. and Mysmenidae gen. sp1 were influenced by edge in the light rain

Table 2.—Summary of GLM testing the effect of four environmental variables on the diversity and total abundance of spiders. Bold values are significant at $P < 0.05$.

Type of model	Response variable Explanatory variables	Estimate	<i>P</i>
Count model	Diversity		
	Average temperature	-0.120	<0.001
	Temperature range	0.080	<0.001
	Seedlings	<0.001	0.020
Count model	Total abundance		
	Average temperature	-0.393	<0.001
	Temperature range	0.253	<0.001
	Seedlings	0.001	0.007
Count model	Dry twigs	<0.001	0.040
	Dry twigs	0.002	0.018

period while neither species was influenced by edge in the heavy rain period. We postulated that these three species are intermediate in sensitivity to environmental change along the edge gradients. Linyphiidae gen. sp1 was found in both the periods of heavy and light rain and showed no edge effect, suggesting that it is insensitive to environmental change along the edge gradients.

This is the first report of an edge effect on the diversity of web builders. The distribution pattern of spider diversity showed an intermediate stage between the positive and negative effects of the edge between rubber plantation and forest. This was consistent across seasons, even though the magnitude of the effect varied seasonally. The positive effect of the edge between rubber plantation and forest was observed in spider abundance in the light rain period. This pattern is in accord with the patterns in abundance of web-building spider assemblage described by Baldissera et al. (2004) and Vander-gast & Gillespie (2004). No edge effects on spider abundance during heavy rains and species richness in both seasonal periods as revealed in the present study are similar to the

results of Baldissera et al. (2008) but different from Baldissera et al. (2004).

Variables influencing the distribution pattern of web-building spiders.—The influence of the temperature range and the average temperature on the diversity and abundance of web-building spiders indicate that both these environmental variables mainly drive spider distribution patterns. Although Chaladze et al. (2014) and Kwon et al. (2014) showed influence of temperature on spiders, those studies did not examine small variations in temperature parameters between sites as in the present study. The response of web-building spiders to small variations in average temperature (26.2–27.3 °C) along the edge gradients observed here suggests the significant importance of temperature for determining spider distribution. In the present study, even though there is a small temperature range (5.7–8.8 °C) along the edge gradients, this is the most important variable positively driving distribution patterns of spider diversity and total abundance. In contrast to our results, Coyle (1981) reported that a wider range of temperatures decreased the diversity and the abundance of web-builders in clear-felled temperate areas. In the present study, the maximum temperature range was 22.5–37.0 °C, and the daily range was typically 8.8 °C in the rubber plantations, which may not be too extreme for spiders. It is possible that the canopy of the rubber plantations alleviates the effect of maximum temperature compared with the clear-felled areas. Based on our results, we postulate that web-building spiders prefer a wider range of temperature within the range of suitable temperatures.

A wider temperature range would support greater diversity and abundance. Different species may require different temperature optima for various essential activities, i.e., web building, prey capture, egg hatching, molting, development (Prestwich 1977; Li & Jackson 1996). Also, different species of spiders need appropriate ranges of ambient temperature to reach and maintain their favorable body temperatures (Krakauer 1972). The longer the activity, the more prey can

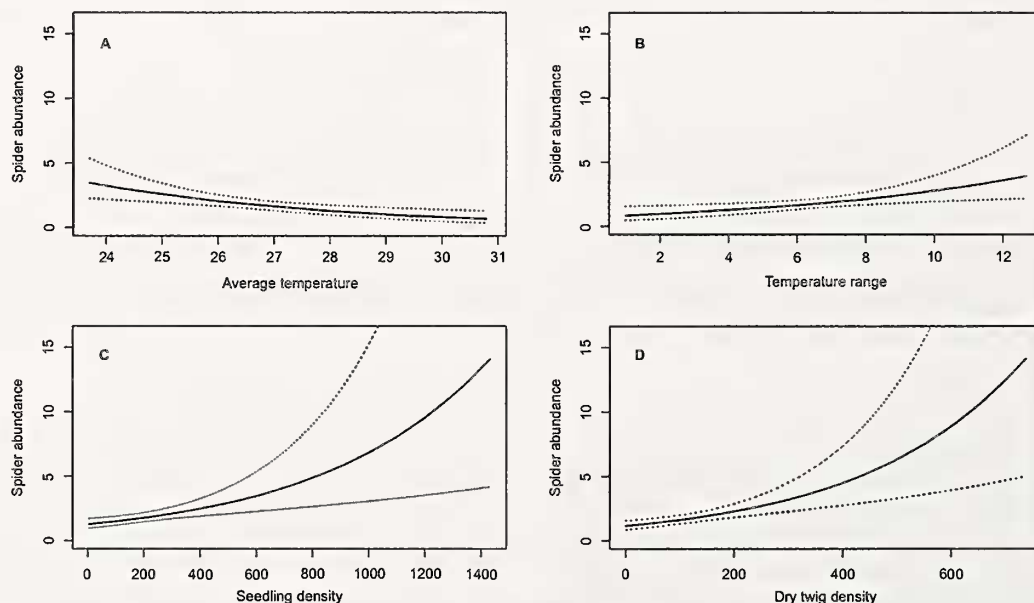


Figure 8.—Plots of the impacts of average temperature (A), temperature range (B), seedlings (C), and dry twigs (D), on the total abundance of web-building spiders of the top models. The solid lines are mean predicted values and the dashed lines indicate 95% confidence intervals.

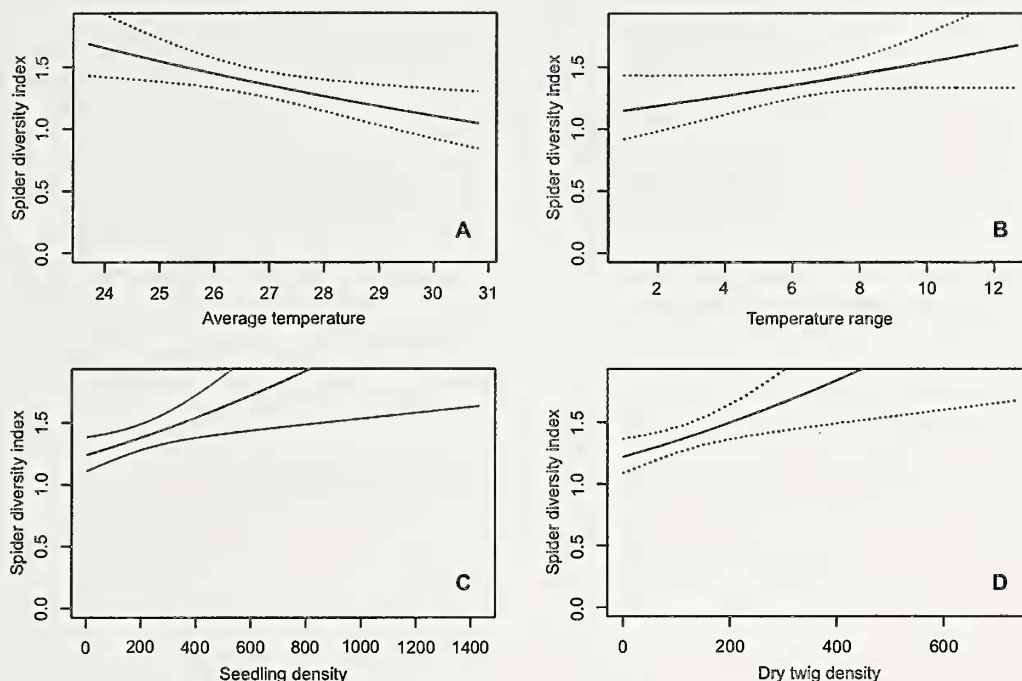


Figure 9.—Plots of the impacts of average temperature (A), temperature range (B), seedlings (C), and dry twigs (D), on the species diversity of web-building spiders of the top models. The solid lines are mean predicted values, and the dashed lines indicate 95% confidence intervals.

be captured and the more food is consumed; this contributes to early production of offspring and increased fecundity (Logan et al. 2006). Additionally, temperature affects silk properties (Yang et al. 2005). Certain spider species need specific temperatures to produce the best quality web, which is associated with the efficiency of prey capture (Barghusen et al. 1997). Previous research suggests that temperature is a significant factor driving distribution patterns of web-building spiders at a local scale (Finch et al. 2008), and our study suggests temperature may also be important on a very fine, microsite scale.

Only density of seedlings and dry twigs positively influenced the distribution patterns of spiders. The positive association with particular characteristics of the understory and spider diversity and total spider abundance is similar to Grill et al. (2005) and Blamires et al. (2007). Notably, the influence of twig density on the patterns also agrees with Gillespie (1987). The present study specifically indicates influence of seedling density on these patterns for the first time. Dry twigs and seedlings here could provide reliable architectural supports for various sizes and types of webs of most spiders (Miyashita et al. 2004) and proper refuges for spiders against their predators such as lizards (Hoffmaster 1982).

Edge effect penetration.—The edge effect between the rubber plantation and the forest was found up to 50 m into the forest during the heavy rain period, and up to 100 m during the light rain period. Thus, the penetration of the edge effect in the light rain period was deeper into the forest than in the heavy rain period. A key variable driving the patterns appeared to be the temperature; this could explain the edge effect being stronger during the dry season (Pohlman et al. 2009). Obvious changes in diversity and total abundance of web-building spiders across very short edge gradients in our

study as compared with those found in beetle communities suggested that web-building spider assemblages could also be an efficient bioindicator of edge effects, especially on a small spatial scale (Ewers & Didham 2008).

Conservation implications.—Certain dominant species were abundant in the forest while others were abundant in the edge or rubber plantations. These patterns suggest that every position along the edge gradients is crucial for harboring particular species of web-building spiders. High diversity and total abundance of web-building spiders in rubber plantations compared to forest in the present study are the result of edge effects, and further study on such patterns in rubber plantation farther from forest is recommended. Since increased seedling and dry twig density in rubber plantations supports higher spider diversity, less disturbance to the understory could reduce losses of spider diversity (Beukema et al. 2007). Generally, for rubber plantations, most farmers frequently clear the understory with herbicides or mechanical cutting. However, a few farmers, who practice agroforest rubber plantation, leave the understory undisturbed and plant more forest tree seedlings. It would be particularly informative to assess spider diversity between these different practices of rubber plantations.

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